

# The larval and post-larval development of the Edible Crab, *Cancer pagurus* Linnaeus (Decapoda: Brachyura)

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## Introduction

The Edible Crab, *Cancer pagurus* Linnaeus occurs from northern Norway (Christiansen, 1969 : 43) to Portugal (Nobre, 1936 : 50); its presence in the Mediterranean requires confirmation (see Zariquiey Alvarez, 1968 : 345-7). In British coastal waters *C. pagurus* is the object of local but important fisheries and in recent years has been subjected to special studies resulting in a greater understanding of its bionomics (see Edwards, 1978). By comparison, the larval development of *C. pagurus* is not well documented. There are several accounts of the first zoeal stage (see below) of *C. pagurus* but the complete larval development has been described superficially by only Lebour (1928), the early stages from laboratory reared material and the later ones from plankton caught specimens.

In 1979 *C. pagurus* was successfully reared to third crab stage in the BM(NH) and from this material the first account of the complete laboratory larval development of this species is now given.

## Materials and methods

The female crab from which the larvae were reared was collected off Shoalstone Point, Devon (SX937568) from a depth of 15 m at a bottom temperature of 10°C in June 1979. The specimen was presented to this Museum by Alan Howard, Fisheries Laboratory MAFF, Burnham-on-Crouch, Essex. The larvae were reared using methods described by Rice & Ingle (1975) and Ingle & Clark (1977). All material was fixed and stored in the preservative formulated by Steedman (1976 : 148) and later transferred to 70% ethanol alcohol. Drawings and measurements were made with the aid of a *camera lucida*. Measurements are as follows: T.T. = total lengths of zoeae measured between tips of dorsal and rostral spines; C.L. = carapace lengths measured from between eyes to posteriolateral carapace margin for zoeae, from rostral tip (for megalopa) and frontal margin (for crab stages) to median posterior carapace margin; the C.W. (= carapace width) of crab stages was taken at the widest part of the carapace.

The female and reared material are deposited in the Collections of the Zoology Department, British Museum (Natural History) registration number 1980 : 121-122.

## Descriptions

### *Cancer pagurus* Linnaeus, 1758

*Cancer pagurus* Thompson, 1828 : Pl. VIII, fig. 1 (1st zoea); Cunningham, 1898 : Pl. 21, figs 1-2 (1st, 2nd crab); Williamson, 1900 : Pl. 1, fig. 4 (1st zoea); 1904 : Pl. 4, figs 71-81 (11 crab stages); Pearson, 1908 : 460, Pl. 13, figs 83-87 (prezoea, 1st zoea); Nordgaard, 1911 : 39, figs 1,2 (1st zoea); Williamson, 1911 : 17, Pl. 4, figs 50-67 (prezoea, 1st zoea); 1915 : 485, figs 307-310 (1st zoea, 1st

crab); Lebour, 1928 : 522, figs 2 (11–15), 4 (22–23), Pl. 1, fig. 10, Pl. 5, fig. 5, Pl. 10, figs 3–5 (1st–5th zoeae, megal., 1st–4th crab); Gurney, 1942 : fig. 38A (5th zoea), fig. 42A (2nd or 3rd zoea); Rice, 1975 : 237, fig. 1 (1st zoea).

#### FIRST ZOEAE

*Dimensions*: T.T. 2.5 mm, C.L. 0.6 mm.

*Carapace* (Fig. 1a): Dorsal spine long, narrowing distally and slightly curved backwards; rostral spine thin, slightly sinuous, slightly shorter than dorsal spine and minutely spinulate; lateral spines long about  $\frac{1}{2}$  carapace length; dorso-median elevation prominent; a pair of antero-median and postero-dorsal setae; posterior margin with 6 short setae.

*Eyes*: Partly fused to carapace.

*Antennule* (Fig. 2f): Unsegmented, with 3 terminal aesthetascs and one short seta.

*Antenna* (Fig. 2a): Spinous process about  $3\frac{1}{2}$  × length of exopod, distal  $\frac{1}{2}$  spinulate; exopod with one terminal spine and 2 setae.

*Mandible* (Fig. 3a): Incisor and molar processes well developed, palp absent.

*Maxillule* (Fig. 3d): Endopod 2-segmented with 1,6 setae; basal endite with 5 setae-spines, coxal with 7 setae-spines.

*Maxilla* (Fig. 4b): Endopod with large outer and smaller inner lobe with 5 + 3 setae; basal endite with large outer and smaller inner lobe, with 4 + 5 setae; coxal endite with large outer lobe bearing 2 long and one short setae and smaller inner lobe with 3 setae one of which is very long and slightly stouter than others; scaphognathite with 4 marginal setae and a very stout posterior plumose projection.

*First maxilliped* (Fig. 6a): Basis with 10 setae arranged 2,2,3,3; endopod 5-segmented with 3,2,1,2,4 + 1 setae; exopod incipiently segmented with 4 terminal plumose setae.

*Second maxilliped* (Fig. 7a): Basis with 4 setae; endopod 3-segmented with 1,1,4 + 1 setae; exopod with 4 terminal plumose setae.

*Third maxilliped*: Not developed.

*Pereiopods*: Not developed

*Abdomen* (Figs 8a, f): 5-segmented + telson; 2nd segment with pair of dorso-lateral processes; postero-lateral margins of all segments rounded 3rd–4th with minute spinules. A pair of minute setae near postero-dorsal margin of segments 2–5. Telson forks long, surfaces minutely spinulate, diverging posteriorly, each with one well developed lateral and one smaller dorsal spine; inner medio-lateral margin of telson with 6 setae, outermost pair with inner margins strongly serrate, median margin of telson strongly convex.

#### SECOND ZOEAE

*Dimensions*: T.T. 2.8 mm, C.L. 0.8 mm.

*Carapace* (Fig. 1b): Lateral spines slightly shorter than in first zoea, posterior margin with 9–10 longer setae.

*Eyes*: Now stalked.

*Antennule* (Fig. 2g): With 4 aesthetascs and one seta.

*Antenna* (Fig. 2b): Unchanged.

*Mandible*: Unchanged.

*Maxillule* (Fig. 3e): Endopod setation unchanged; outer margin of basal endite with a prominent plumose seta, distal margin with 7 setae-spines; coxal setation unchanged.

*Maxilla* (Fig. 4c): Endopod, basal and coxal setation unchanged; scaphognathite with 10 plumose setae of equal length.

*First maxilliped* (Fig. 6b): Basal and endopod setation unchanged; exopod with 6 terminal plumose setae.

*Second maxilliped* (Fig. 7b): Basal and endopod setation unchanged; exopod with 6 terminal plumose setae.

*Third maxilliped*: Not developed.

*Pereiopods*: 1–4 present as undifferentiated buds.

*Abdomen* (Fig. 8b): Postero-lateral margins of segments 3–4 with incipient acute processes; telson forks longer than in first stage.

## THIRD ZOEAE

*Dimensions*: T.T. 3.7 mm, C.L. 1.0 mm.

*Carapace* (Fig. 1c): With minute setules on dorsal spine; lateral spines slightly smaller than in previous stage.

*Eyes*: Unchanged.

*Antennule* (Fig. 2h): With 4 aesthetascs and 2 setae.

*Antenna* (Fig. 2c): Spinous process slightly less than  $3\frac{1}{2}$  × length of exopod; endopod now developed as a broad bud.

*Mandible*: Unchanged.

*Maxillule* (Fig. 3f): Endopod setation unchanged; basal endite with 8–9 setae-spines in some specimens, additional setae very small; coxal setation unchanged.

*Maxilla* (Fig. 4d): Endopod and basal endite setation unchanged; outer lobe of coxal endite with 4 setae inner lobe unchanged; scaphognathite with 17 setae.

*First maxilliped* (Fig. 6c): Basal and endopod setation unchanged; exopod with 8 terminal plumose setae.

*Second maxilliped* (Fig. 7c): Basal and endopod setation unchanged; exopod with 8 terminal plumose setae.

*Third maxilliped*: Represented as a small bud.

*Pereiopods*: Buds longer than those of previous stage, 5th pair now present as small buds.

*Abdomen* (Fig. 8c): 6th segment now present and almost differentiated from telson; spinous process on postero-lateral margins of segments 3–4 now conspicuous; inner medio-lateral margin of telson with 8 setae. Pleopods represented as small buds on segments 2–5.

## FOURTH ZOEAE

*Dimensions*: T.T. 4.3 mm, C.L. 1.2 mm.

*Carapace* (Fig. 1d): Dorsal and rostral spines slightly stouter than in previous stage and lateral spines smaller; posterior margin of carapace with 11–12 setae.

*Eyes*: Unchanged.

*Antennule* (Fig. 2i): Setal formula unchanged but aesthetascs slightly stouter than in previous stage.

*Antenna* (Fig. 2d): Spinous process less than  $3\frac{1}{2}$  × length of exopod; endopod bud subequal to exopod.

*Mandible* (Fig. 3b): Outer lip of incisor formed by a prominent row of broad tubercles merging into continuous margin.

*Maxillule* (Fig. 3g): Endopod setation unchanged; basal endite with 10–11 setae-spines; coxal endite with 8 setae-spines.

*Maxilla* (Fig. 5a): Endopod setation unchanged; outer lobe of basal endite unchanged, inner lobe with 6 setae; coxal endite unchanged; scaphognathite with 22 setae.

*First maxilliped* (Fig. 6d): Basal setation unchanged; endopod terminal segment with 6 setae; exopod with 10 distal plumose setae.

*Second maxilliped* (Fig. 7d): Basal and endopod setation unchanged; exopod with 10 distal plumose setae.

*Third maxilliped*: Now with a small exopod.

*Pereiopods*: Longer than in previous stage and incipiently segmented; dactylus differentiated on cheliped.

*Abdomen* (Figs 8d, g): 6th segment clearly demarcated from telson; postero-lateral spinous processes on segments 3–5 longer than in previous stage; telson inner medio-lateral margin with 10 setae. Pleopod buds longer than in previous stage.

## FIFTH ZOEAE

*Dimensions*: T.T. 4.7 mm., C.L. 1.4 mm.

*Carapace* (Fig. 1e): Setules on dorsal spine and setae on posterior margin of carapace longer than in previous stage, lateral spine smaller.

*Eyes*: Unchanged.

*Antennule* (Fig. 2j): Endopod present as a small bud; exopod with 6 aesthetascs and 4 setae.



*Antenna* (Fig. 2e): Spinous process  $\times 3$  length of exopod; endopod varying from  $\frac{1}{2}$  to over  $\frac{3}{4}$  length of spinous process and, in some specimens, incipiently segmented.

*Mandible* (Fig. 3c): Inner margin of incisor process clearly defined as a ridge; mandibular palp present as a small bud.

*Maxillule* (Fig. 4a): Endopod setation unchanged; basal endite with 13–14 setae-spines; coxal endite with 10 setae-spines.

*Maxilla* (Fig. 5b): Endopod setation unchanged; outer lobe of basal endite with 6–7 setae, inner with 7 setae; outer lobe of coxal endite unchanged, inner lobe with 3–4 setae; scaphognathite with 31 setae.

*First maxilliped* (Fig. 6e): Basal and endopod setation unchanged; exopod with 12 distal plumose setae.

*Second maxilliped* (Fig. 7e): Basal and endopod setation unchanged; exopod with 12 distal plumose setae.

*Third maxilliped*: Endopod clearly segmented.

*Pereiopods*: Cheliped well formed, those of 2–5 clearly segmented.

*Abdomen* (Figs 8e, h): Telson forks less divergent than in previous stages; lateral processes on 2nd segment smaller. Pleopod buds long and now present on 6th segment.

## MEGALOPA

*Dimensions*: C.L. 2.4 mm.

*Carapace* (Figs 9a, b): Longer than broad, narrowing anteriorly; frontal region (f) with slight median furrow, orbital margin expanded; rostrum long, terminally acute and horizontally directed, hepatic regions (h) inflated, protogastric (p) each with a raised carina, epibranchial (e) and mesobranchial (m) regions defined by a carina, cardiac region with a long posteriorly directed horizontal spine.

*Eyes*: Large, elongated.

*Antennule* (Fig. 10a): Peduncle indistinctly 3-segmented, 2nd segment with 1–2 short setae; exopod 4-segmented, 2nd with 8 and 3rd with 4 aesthetascs and 1 seta, 4th with 1 terminal and 1 subterminal seta; endopod with 4 terminal and 1 subterminal setae.

*Antenna* (Fig. 10b): Peduncle with 3 segments; flagellum 6-segmented, setal formula (from distal to proximal) 4,3,0,4,3,0,2,1,1,1.

*Mandible* (Fig. 10c): Molar and incisor parts not distinguishable one from the other, disto-internal angle acutely produced; mandibular palp 3-segmented, terminal segment longest with 7 distal setae.

*Maxillule* (Fig. 10d): Endopod now unsegmented and with 4 setae; basal endite with 21 setae-spines; coxal endite with 13–14 setae.

*Maxilla* (Fig. 10e): Endopod now reduced to acute lobe, unarmed; basal endite with 8 + 9 setae, with 3–4, 5 setae; scaphognathite with 48–49 plumose setae shorter than in last zoeal stage.

*First maxilliped* (Fig. 11a): Coxal segment partly differentiated from basis and with 11–12 setae on inner margin, basis with 19–22 setae; endopod unsegmented with 4 setae on outer margin and 4 apical setae; exopod 2-segmented, proximal with 2 disto-external setae and terminal segment with 4 apical setae; epipod well developed and with 4–5 setae.

*Second maxilliped* (Fig. 11b): Coxal and basal segments undifferentiated with 0–2 setae on inner margin; endopod carpus (antipenultimate segment) with 1 disto-internal seta, propodus with 5 disto-external setae, dactylus with 5 spines and 5 setae; exopod 2-segmented, terminal segment with 4 long setae; epipod short and broad.

*Third maxilliped* (Fig. 11c): Basis with 2 setae on internal margin and differentiated from coxa; endopod, ischium with 3–4 setae on outer surface and 13–14 setae placed on or near inner margin that also bears acute tubercles, merus with 2–3 outer disto-external setae and 3 setae on internal margin, carpus with 1 disto-external and 3 disto-internal setae, propodus with 2 disto-external setae and 4 setae on internal margin, dactylus with 7 setae; exopod 2-segmented, distal segment with 4 setae; epipod bifurcate, longest branch with 13–14 setae that extend onto coxal surface.



*Pereiopods* (Figs 12 a-e): Cheliped stout, with a prominent ischial spine, inner distal propodal margin with 4 blunt teeth, inner dactylar margin with at least 2 indistinct teeth. Pereiopods 2-5 relatively stout, coxa of 2nd (Fig. 12b) with acute process, dactylus of 5th pereiopod with 3 long terminal setae.

*Abdomen* (Figs 9a,c,d, 12h): With 6 segments + telson; postero-lateral margins of 2nd-5th broadly truncate and 3rd-5th minutely spinose; a small pair of dorso-median setae present near posterior margins of segments 2-6 along with other setae as shown. Telson (Fig. 12h) broader than long, with three pairs of dorso-median setae and a pair of setae on posterior margin. Five pairs of pleopods, distal segment of pleopod exopods with long plumose marginal setae, 1st (Fig. 12f) with 16, 2nd 15-16, 3rd 15-17, 4th (Fig. 12g) and 5th (uropods, Fig. 12h) with 8 setae respectively, endopods of pleopods 1-4 with 3 distally placed coupling hooks on internal margins.

#### FIRST CRAB

*Dimensions*: C.L. 2.3 mm., C.W. 2.4 mm.

*Carapace* (Fig. 13a): Maximum width at about 4th pair of antero-lateral teeth. Dorsal surface minutely denticulate, protogastric and meso-metabranial regions slightly inflated and with long setae; frontal and orbital margins irregularly denticulate; antero-lateral margin setose, with 4 large bi- or tridentate teeth with additional spines between them; postero-lateral and posterior margin of carapace setose. Eyestalks with 2-3 spines.

#### SECOND CRAB

*Dimensions*: C.L. 2.9 mm., C.W. 3.9 mm.

*Carapace* (Fig. 13b): Maximum width now at about 7th antero-lateral tooth. Denticles smaller than in 1st stage and marginal setae almost wholly absent; antero-lateral margins with 8-9 spinose teeth.

#### THIRD CRAB

*Dimensions*: C.L. 3.7 mm., C.W. 4.9 mm.

*Carapace* (Fig. 13c): Denticles now very small; antero-lateral margins now with 9 defined, obtusely serrate teeth and one postero-lateral tooth. Spines on eyestalks reduced.

### Variation

The material reared for this present study agrees with previously published accounts of *C. pagurus* larvae except for the minor details listed in Table 1 in which the various available descriptions of the 1st zoeal stage are compared. In addition, Lebour (1928 : 523) described the fourth zoea as having 'two pairs of extra internal spines to telson' compared with one extra pair acquired at this stage by the present specimens. Gurney (1942, figs 38A & 42A) figured the maxillule and 1st-3rd maxillipeds of *C. pagurus*. His figure of the maxillule can be attributed to the fifth stage zoea but lacks a seta on the first segment of the endopod whilst the basis of the first maxilliped (perhaps of a 2nd or 3rd stage) has only three setae and an endopod setal formula of 0,2,1,2,2, on the first and 1 + 4 on the second and with the exopods of both pairs with 7 terminal setae.

Samples of *C. pagurus* zoeae collected in the southern N. Sea, at 53°50'N: 1°00'E from 6-17 July 1976, were compared with the present laboratory reared material. Stages IV and V of the N. Sea samples were found to be considerably larger (i.e. T.T. ZIV 4.7 mm; ZV 5.6 mm) than the reared specimens (i.e. ZIV 4.3 mm; ZV 4.7 mm) and a small percentage of the first zoeae of the plankton specimens was found to have one or both telson forks bifurcated and, in some, an extra medio-lateral telson spine was present as shown in Fig. 13e. In this figured specimen the lateral spine on the right fork of the telson and the small lateral and dorsal spine are absent; an extra small spinule is developed on the left outer bifurcation

and the seta on the basal segment of the maxillule endopod is also bifurcated. It is not known if these abnormalities are of genotypic or phenotypic origin.

### Distinguishing features of *C. pagurus* larvae

From the present larval account of *C. pagurus* it may now be possible to distinguish the zoeae of this species from the early zoeal stages described of many other brachyryhynch crabs that occur in British coastal waters using the following combined features. (1) In *C. pagurus* only the second segment of the abdomen is armed with a pair of dorso-lateral processes. Early zoeal stages of *Polybius henslowii* Leach, *Bathynectes longipes* (Risso), *Liocarcinus* (= *Macropipus*) spp., *Goneplax rhomboides* (Linnaeus), *Geryon tridens* Kroyer, *Pilumnus hirtellus* (Linnaeus), *Xantho incisus* Leach, *Monodaeus couchi* (Couch), *Pinnotheres pisum* (Linnaeus) and *P. pinnotheres* (Linnaeus) have dorso-lateral processes on more than one segment. (2) *C. pagurus* has lateral spines on the carapace; these are absent in zoeae of *C. maenas* (Linnaeus) and *Portumnus latipes* (Pennant). (3) *C. pagurus* zoeae have two dorso-lateral spines on each telson fork; the zoeae of *Corystes cassivelaunus* (Pennant) and *Thia scutellata* (Fabricius) have only one spine. (4) *C. pagurus* zoeae have smooth postero-lateral margins to the abdominal segments except in the first zoeal stage when these margins may have a few very minute spinules. The zoeae of *Pirimela denticulata* has conspicuously denticulate postero-lateral margins. (5) In *C. pagurus* the outer pair of telson mesio-lateral spines have strongly serrate outer margins. By comparison these serrations are far less developed in zoeae examined belonging to *Liocarcinus* spp., *C. maenas*, *X. incisus*, *M. couchii*, *P. hirtellus* and *G. tridens*.

Zoeae of *C. pagurus* are separated less satisfactorily from those of *Atelecyclus rotundatus* (Olivi) by having a relatively straight dorsal spine on the carapace, three distal 'setae' on the antennal exopod and 1,6 setae respectively on the endopod segments of the maxillule. Lebour (1928 : 524, fig. 4, 1-5, 26) described the zoeae of *A. rotundatus* as having a curved dorsal carapace spine in the early stages, two distal setae on the antennal exopod and 1,4 setae on the respective segments of the maxillule endopod. Rice (1980 : 336) has included the following two characters in his larval diagnosis of the subfamily Atelecyclinae (to which *A. rotundatus* belongs). (a) A maxillule endopod with 1,6 setae; (b) the diminutive size of the middle seta of the distal two groups of three on the first maxilliped basis. These two subfamilial features are based entirely upon the zoeal descriptions of *Erimacrus* and *Telmessus* and their confirmation in larvae belonging to *Atelecyclus* will have to await further laboratory rearing and descriptions of larvae belonging to this genus, particularly of *A. rotundatus*, to establish the features for separating *Atelecyclus* larvae from those of *C. pagurus*.

An additional feature that may prove of value for separating the early zoeal stages of *C. pagurus* from corresponding stages of other species is the exceedingly long spine on the inner lobe of the coxa of the maxilla (see Fig. 13e). A spine of this proportion is depicted for *C. magister* Dana by Poole (1966, fig. 1g). This corresponding spine on the coxa of the maxilla of zoeae I,II of *C. maenas*, *Liocarcinus* spp., *G. tridens*, *X. incisus* and *M. couchi* never overreaches the other coxal spines as seen in *C. pagurus* (cf. figs 13 d & e).

The megalopa of *C. pagurus* has a prominent cardiac spine on the carapace that separates it from megalopae of *Liocarcinus* spp., *P. henslowii*, *C. maenas*, *Xaiva biguttata* (Risso), *T. scutellata*, *P. denticulata*, *G. tridens*, *G. rhomboides*, *P. hirtellus*, *X. incisus*, *M. couchi* and *Pinnotheres* spp. The narrow styliiform dactylus of the 5th pereopod and the presence of 8 uropodal setae distinguishes the megalopa of *C. pagurus* from that of *P. latipes* in which the 5th pereopod dactylus is lanceolate, the uropods have only 7 setae and the dorsal spine on the carapace arises from the meta- or urogastric regions and is thus further forward than in *C. pagurus* (see Lebour, 1944: fig. 3 d). The absence of spines on the submedian and hepatic regions of the carapace and the presence of 3 setae on the dactylus of the 5th pereopod separate the megalopa of *C. pagurus* from that of *C. cassivelaunus*; the latter species has

submedian and hepatic spines (as well as a pair of minute protogastric spinules) and the 5th pereopod dactylus has only 2 setae (see Ingle & Rice, 1971: figs 7F & 8).

Further studies are required to establish satisfactory features for separating the megalopa of *C. pagurus* from that of *A. rotundatus*. Lebour (1928: 525, Pl. IX, fig. 5) states that the megalopa of *A. rotundatus* has 10–11 uropodal setae (*C. pagurus* has 8 setae), and depicts 4–5 setae on the 5th pereopod dactylus (*C. pagurus* has only 3 setae).

### Comparisons of larvae of the species of *Cancer*

The first zoeal stage of eleven and the complete larval development of eight species of *Cancer* have been described. The majority of these accounts omit details of features such as carapace setation of the zoeae, lateral spines of the telson, the armature of the megalopal carapace, proximal segments of the pereopods and setation of the telson. Distinctive larval features described in these various accounts are summarized in Tables 2–4. No single character (except perhaps the exceedingly large size and exceptionally large number of setae on the antennule and scaphognathite in later stages of *C. magister* and the presumably 5-segmented abdomen described for all stages of this species (see Poole, 1966)) can be used to separate the known species of *Cancer* larvae, but they appear to be identifiable on combined features. A comparison of the first zoeal stages of Pacific and Atlantic species of *Cancer* suggest that those from the former region have more pronounced postero-lateral spines on the abdominal segments and a tendency to fewer antennular aesthetascs-setae. Zoo-geographic differences are more obvious when the fifth zoeal stages are compared. Pacific species have a maximum of 6 setae on the maxilla endopod; this number is always 8 in Atlantic species except for *C. ? bellianus* that has 7 setae. There are never more than 9 setae on the 1st maxilliped basis in Pacific zoeae compared with 10 or more in Atlantic ones.

Rice (1975 & 1980: 331) recognized trends towards the existence of two possible groups of *Cancer* zoeae with respect to the armature of appendages: (a) species with 2 setae on the basal segment of the endopod of the first maxilliped, the maxillule endopod segments armed with 1,5 setae respectively and the endopod of the maxilla with 6 setae; (b) species with 3 setae on the basal segment of the endopod, 1,6 setae on the maxillule endopod and the endopod of the maxilla armed with 7–8 setae. This present study also suggests that zoeae attributable to group (a) have only 2 and those in group (b) 3 terminal 'spines' on the antennal exopod. Zoeae in which the above mentioned features are not combined are *C. amphioetus*, *C. gibbosulus*, *C. porteri* and zoea V of *C. ? bellianus*.

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**Table 1** Comparative features of first zoeal stage of *Cancer pagurus* after various authors and compared with the present material

Features	Williamson 1900 : 1911	Pearson 1908	Norgaard 1911	Lebour 1928	Rice 1975	Present material
Length of dorsal to rostral spine:	slightly longer	much shorter	longer	equal to	longer	slightly longer
Spinulation of dorsal spine:	well developed	not shown	distally	not shown	absent	absent
Spinulation of rostral spine:	well developed	not shown	not shown	not shown	minute	minute
Setae + aesthetascs on antennule:	5	4	?	?	3-4	4
Antennal spinous process to rostral length:	much more than half	about half	slightly less than half	?	less than half	slightly more than half
Antennal exopod to spinous process length:	slightly less than half	about one third	about one third	about one third	slightly less than one third	slightly less than one third
Maxillule, spines-setae on coxa:	7	-	-	6	-	7
Maxilla, spines-setae on endopod outer lobe:	5 + one minute seta	-	-	4	5 (or 4)	5
Maxilla, spines-setae on coxal endite:	6 ? + 3	-	-	total of 5	3 + 3	3 + 3
Second maxilliped, setae on basis:	3	-	-	-	4	4
Second maxilliped, endopod setae:	0, 1, 5 + 1	-	-	-	1, 1, 5 + 1	1, 1, 4 + 1
Abdominal segments, spinules on postero-lateral margins:	present on 2-5	not shown	not shown	not shown	not shown	present on 3-4



**Table 2** Comparative features of first zoeal stages of eleven *Cancer* species after: 1 Present material & Rice 1975; 2 Connolly 1923; 3 Sastry 1977a; 4 Sastry 1977b; 5 Fagetti Guaita 1960; 6 Aikawa 1937; 7 Mir 1961; 8 Poole 1966; 9 Roesjaji 1976; 10 Trask 1974; 11 Anderson 1978; 12 Rice 1975; 13 Trask 1970; 14 Ally 1975; 15 Iwata 1973.  $\leq$  = slightly or much less than  $\geq$  = slightly greater or equal to, \* = approx. lengths calculated from illustrations

	ATLANTIC					PACIFIC					
	<i>C. pagurus</i> 1	<i>C. irroratus</i> 2,3	<i>C. borealis</i> 4	<i>C. porteri</i> 5	<i>C. gibbosulus</i> 6	<i>C. magister</i> 7,8	<i>C. antennarius</i> 7,9	<i>C. anthonyi</i> 10,11,12	<i>C. productus</i> 13	<i>C. gracilis</i> 14	<i>C. amphioctus</i> 15
Dorsal spine/Carapace length:	$\geq$ x2 4	$\geq$ x1 5 <sup>1</sup> 4 <sup>1</sup>	$\geq$ x1 4	$\geq$ x1 4	$\geq$ x1 ?	$\leq$ x1 3	$\geq$ x1 3-4	$\geq$ x1 3	$\geq$ x1 3	$\geq$ x1 5	$\leq$ x1 3
Antennule, aesthetascs-setae:											
Antenna, exopod distal spines:	3	3	3	3	2	3	2	2	3	2	2
Maxillule, endopod setae:	1.6	1.6	1.6	1.5	1.6	1.6	1.4	1.5	1.6	1.5	1.6
Maxillule, basis, coxa, setae-spines:	5.7	5.7	5.6	5.4	5.7	5.6	5.6	5.6	5.6	5.7	5.6
Maxilla, endopod, basis; coxa, setae-spines:	5+3,4+3, 3+3	4+3,3+5, 3+3	5+3,4+5, 3+3	4+3,4+4, 3+3	3+3,4+4, 3+3	4+3,4+5, 4+3	3+3,4+5, 5 <sup>1</sup> or 3+3 <sup>2</sup>	4+2,4+4, 3+3 <sup>1</sup>	4+3,4+5, 4+3	3+3,4+5, 3+3	3+3,4+4, 3+4
Maxilla scaphognathite:	4+1	4+1	4+1	4+1	4+1	3+1	3+1	4+1	4+1	4+1	4+?1
First maxilliped basis, setae:	10	5 <sup>1</sup> 9 <sup>1</sup>	9	9	?	9	9	4+1 8	10	9	8
First maxilliped endopod, setae:	3,2,1,2, 4+1	3,2,1,2, 4+1	3,2,1,2, 4+1	3,2,1,2, 4+1	?	3,2,1,2, 4+1	2,2,1,2, 4+1	2,2,1,2, 4+1	3,2,1,2, 4+1	2,2,1,2, 4+1	2,2,2,2, 4+1
Abdominal segments, postero-lateral margins:	3-4 obtuse minutely spinulate	2-4 obtuse <sup>1</sup>	1-5 obtuse	3-5 spinose	4-5 slightly spinose	1-5 spinose	3-5 <sup>10</sup> slightly spinose	3-5 <sup>10</sup> slightly spinose	1-5 slightly spinose	2-5 slightly spinose	3-5 obtusely spinose
Length* carapace vertex to telson tips:	1.8 mm	1.5 mm	1.2 mm	1.5 mm	1.4 mm	2.5 mm	1.3 mm	1.2 mm	1.8 mm	1.2 mm	1.7 mm

**Table 3** Comparative features of fifth zoeal stages of nine *Cancer* species. \*See legend to Table 2 otherwise 1 Frost 1936: 2 Rice & Williamson 1977

	ATLANTIC				PACIFIC				
	<i>C. pagurus</i>	<i>C. irroratus</i>	<i>C. borealis</i>	<i>C. bellianus</i>	<i>C. magister</i>	<i>C. antennarius</i>	<i>C. anthonyi</i>	<i>C. productus</i>	<i>C. gracilis</i>
*Authors:				2					
Dorsal spine/carapace length:	$\geq x+1$	$\leq x+1$	$\geq x+1$	$\geq x+1$	$\geq x+1$	$\geq x+1$	$\geq x+1$	$\geq x+1$	$\geq x+1$
Antennule, aesthetascs-etae:	10	25	13	11	29	14	20 <sup>10</sup> 17 <sup>11</sup>	24	25-26
Antenna, exopod distal spines:	3	3	3	broken	3	2	2	3	2
Maxillule, endopod setae:	1,6	1,6	1,6	1,5	1,6	1,5	1,5	1,6	1,5
Maxillule, basis, coxa, setae-spines:	14,10	18,10	12,10	not described	21-23,16	14,7	16,11 <sup>10</sup>	17,10	15,10
Maxilla, endopod, basis, coxa setae-spines:	5+3,7+7, 4+4	5+3,10+8, 5+5	5+3,7+7, 4+3	endopod 3+4 basis, coxa not described	4+3,14+12, 5+5	3+3,8+8, 3+3	3+3,8+7 <sup>10</sup> 4+4, 3+3,7+8 <sup>11</sup> , 4+4	4+3,8+8, 4+4	3+3,7+7 or 7+8, 4+4
Maxilla scaphognathite setae:	31	37-38	29	36-37	49-50	34-35	34-36 <sup>10</sup> 32-36 <sup>11</sup>	37-38	33-36
First maxilliped basis, setae:	10	12	10	10	9	9	3 <sup>10</sup> 8 <sup>11</sup>	8	9
First maxilliped endopod, setae:	3,2,1,2, 5+1	3,2,1,2, 5+1	3,2,1,2, 5+1	3,2,1,2, 5+1	3,2,1,2, 5+1	2,2,1,2, 5+1	2,2,1,2, 4+1 <sup>10</sup> 2,2,1,2, 5+1 <sup>11</sup>	3,2,1,2, 5+1	2,2,1,2, 5+1
Second maxilliped basis, setae:	4	3	5	4	4	4	4	4	4
Second maxilliped endopod, setae:	1,1,4+1	1,1,6+1	1,1,4+1	1,1,4+1	1,1,4+1	1,1,4+1	1,1,6+1 <sup>10</sup> 1,1,4+1 <sup>11</sup>	1,1,4+1	1,1,4+1
Abdominal segments:	6	6	6	6	5	6	6	5	6
Abdominal segments spinosised postero-lateral margins:	3-5	3-5	2-5	3-5	2 (minute) 3-5	3-5	3-4 <sup>10</sup> 1-6 <sup>11</sup>	3-5	2 (minute) 3-4
Length, carapace vertex to telson tips:	4.4 mm	3.2 mm	4.2 mm	5.2 mm	9.0 mm	4.0 mm	3.1 mm	4.0 mm	3.3 mm

**Table 4** Comparative features of megalopae of eight *Cancer* species after various authors in Table 2

	<i>C. pagurus</i>	<i>C. irroratus</i>	<i>C. borealis</i>	<i>C. magister</i>	<i>C. antennarius</i>	<i>C. anthonyi</i>	<i>C. productus</i>	<i>C. gracilis</i>
Antennule exopod, aesthetascs-setae:	15	26	22	41	20	22-27 <sup>10</sup> 32 <sup>11</sup>	30	34
Antennule endopod, setae:	4	6	4	9	5	5 <sup>10</sup> 7 <sup>11</sup>	5	6
Antenna segments:	10	10	11	12	11	11	11	10-11
Antennal setae, proximal to distal:	4,3,0,4,3,0, 2,1,1,1	4,4,6,0,3 0,4,2,2,0	5,4,0,3,0, 5,0,0,3,1,0	5,5,2,6,0, 7,2,0,8,1,1, 11,0	4,4,0,5,0,4, 0,0,4,2,4,	4,4,0,4,0,4, 0,0,4,2,2, <sup>10</sup>	5,3,1,3,2,3, 0,0,4,4,5,	5,4,0-1,5,0,4,3-5, 0,0,4-5,2-3,5
Mandibular palp, setae:	7	9	9	17	9	5,5,0,5,0,4, 0,0,3,2,5, <sup>11</sup> 7 <sup>10</sup> 13 <sup>11</sup>	12	8
Maxillule endopod, setae:	0,4	1,6	1,5?	0,5	1,5	1,5 <sup>10</sup> 1,3 <sup>11</sup>	0,4	1,2
Maxillule basis; coxa, setae:	21,14	23,10	14,11	38-43,29-31	17,11	20,8 <sup>10</sup> 26-28,16 <sup>11</sup>	30-32,15-17	26,14-15
Maxilla scaphognathite, setae:	48-49	46	44-45	110-124	53-55	45-50 <sup>10</sup> 47-53 <sup>11</sup>	62-64	53-59
Second maxilliped endopod, setae of three distal segments:	1,5,10	2,6,8	1,7,8	6,20,13	0,7,8	0,5,10 <sup>10</sup> 1,7,10 <sup>11</sup>	0,7,7	1,5-7,8-9
Third maxilliped exopod, setae:	0,4	3,6	0,5	17,10	0,5	0,6 <sup>10</sup> 3,6 <sup>11</sup>	5,6	2-4,5
Pleopods 1-3 exopod, setae:	16,15-16,15- 17,14-15	15,15,13, 11	16,16,16, 16	32,32,32, 28	19,18,19, 15	16,16,14, 1 <sup>10</sup> 16-17,17-18 16-17,15-16 <sup>11</sup>	21,19,19, 19	17-19,17-19, 17-18,14-16
Abdominal segments:	6	6	6	5	6	6	5	6
Uropods exopod, setae:	8	9	10	22	9	7 <sup>10</sup> 9-10 <sup>11</sup>	12	7-9
Total lengths:	3-4 mm	3-7 mm	4-2 mm	11 mm	3-8 mm	4-0 mm	6-0 mm	3-2 mm



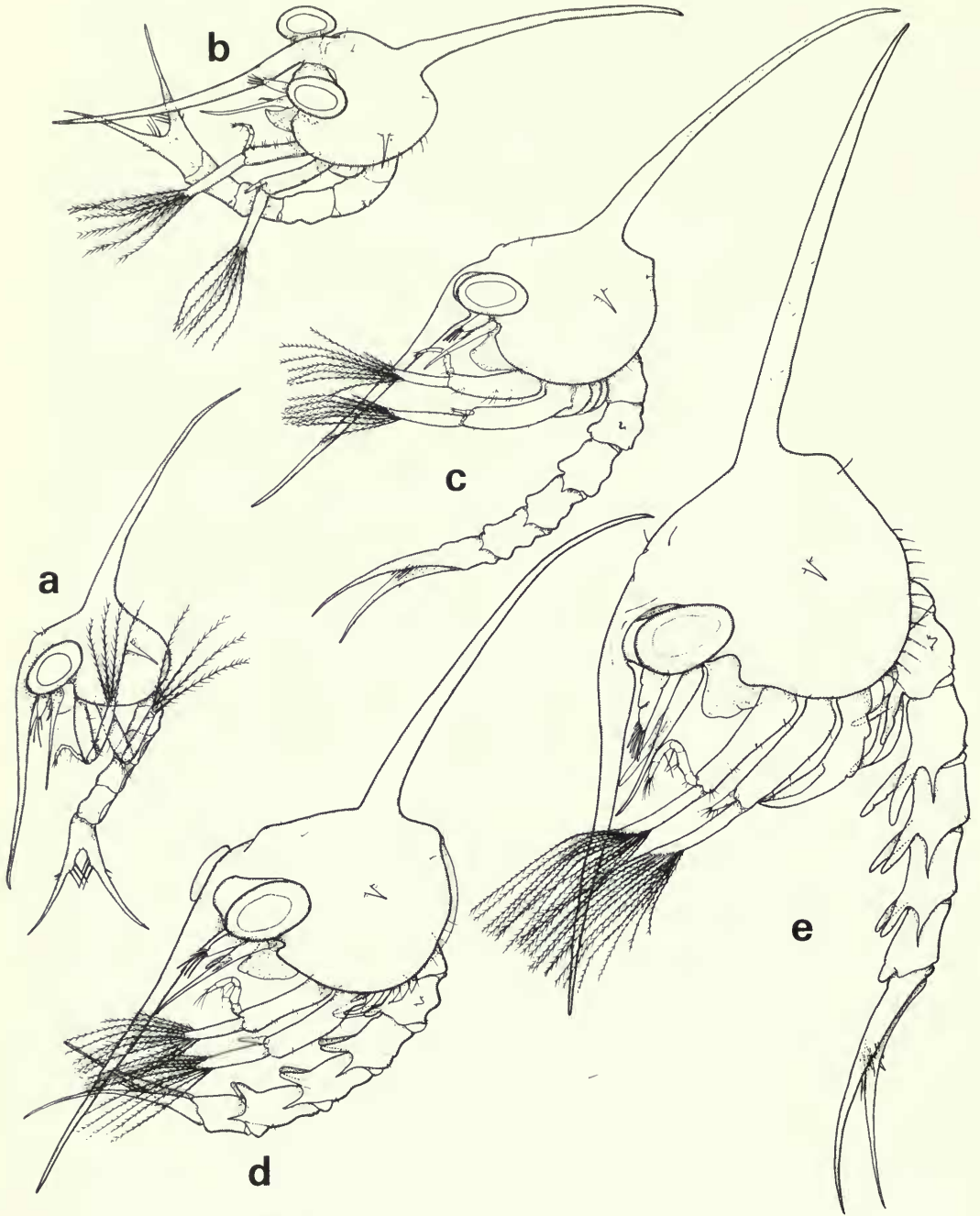
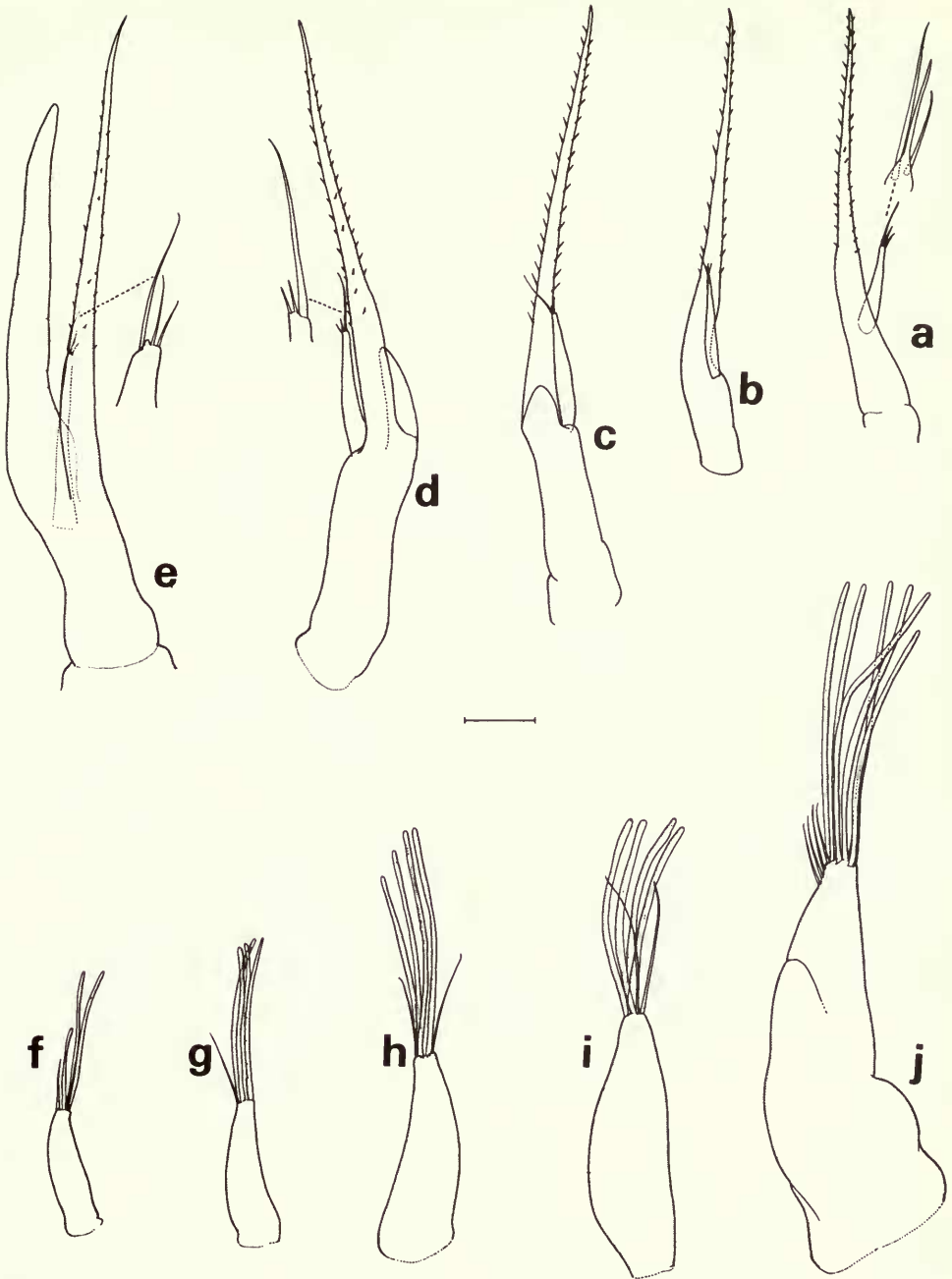
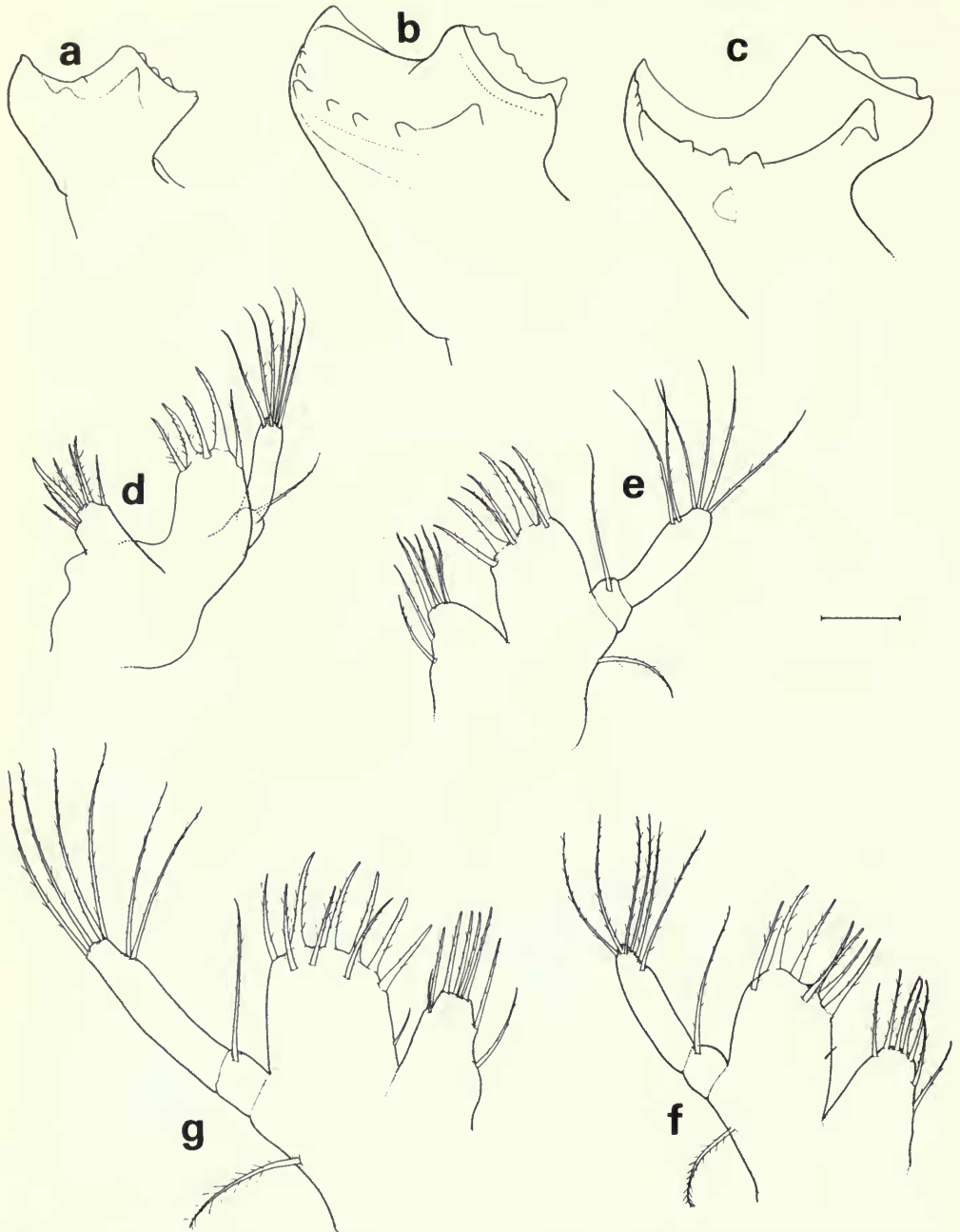


Fig. 1 *Cancer pagurus* L.: a-e 1st-5th zoeae.



**Fig. 2** *Cancer pagurus* L.: a-e antennule; f-j antenna of 1st-5th zoeae; scale = 0.1 mm.



**Fig. 3** *Cancer pagurus* L.: a-c right mandible of 1st, 4th, 5th zoeae; d-g maxillule of 1st-4th zoeae; scale = 0.05 mm.



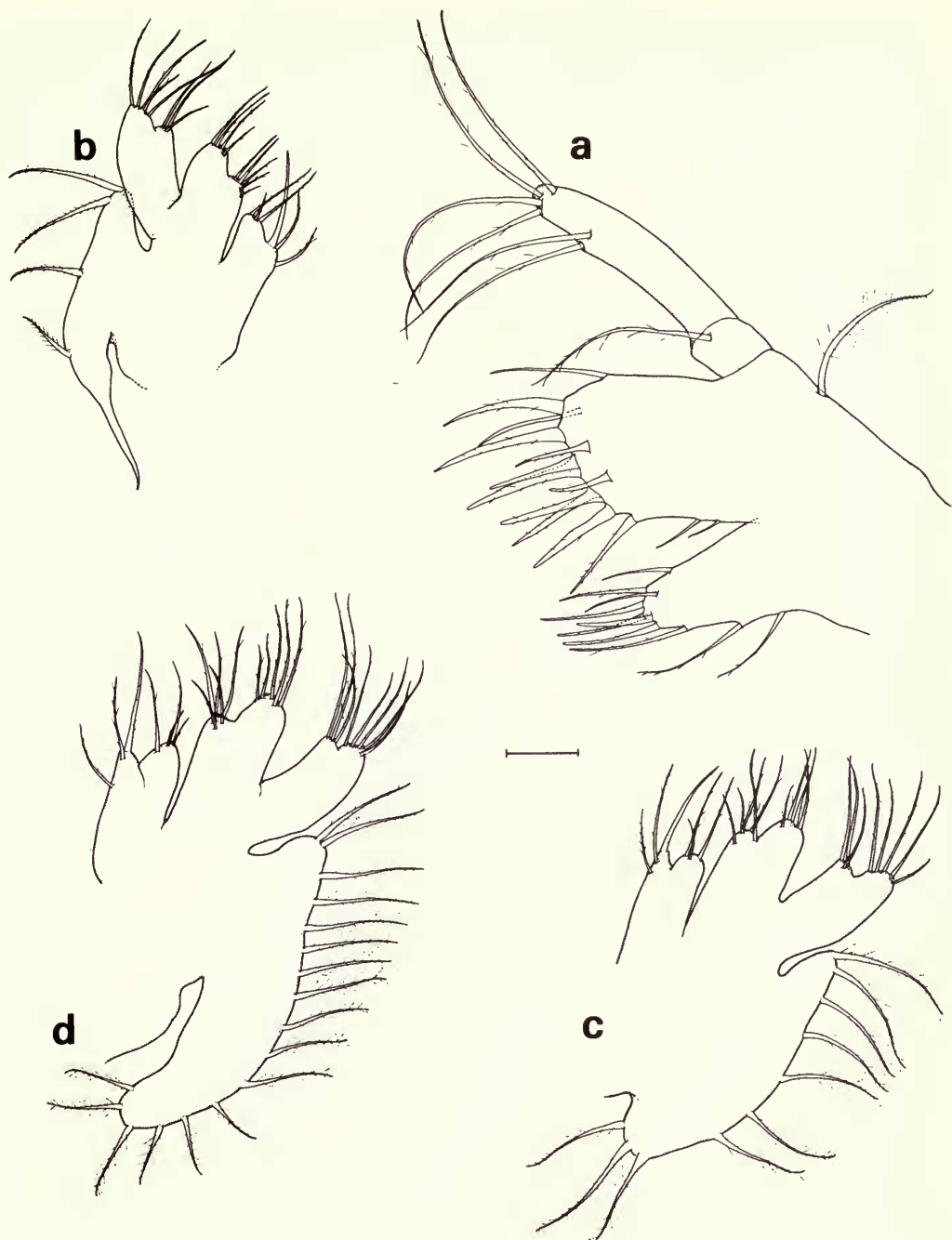


Fig. 4 *Cancer pagurus* L.: a maxillule 5th zoea; b-d maxilla 1st-3rd zoeae; scale = 0.05 mm.



Fig. 5 *Cancer pagurus* L.: a-b maxilla 4th & 5th zoeae; scale as Fig. 4.

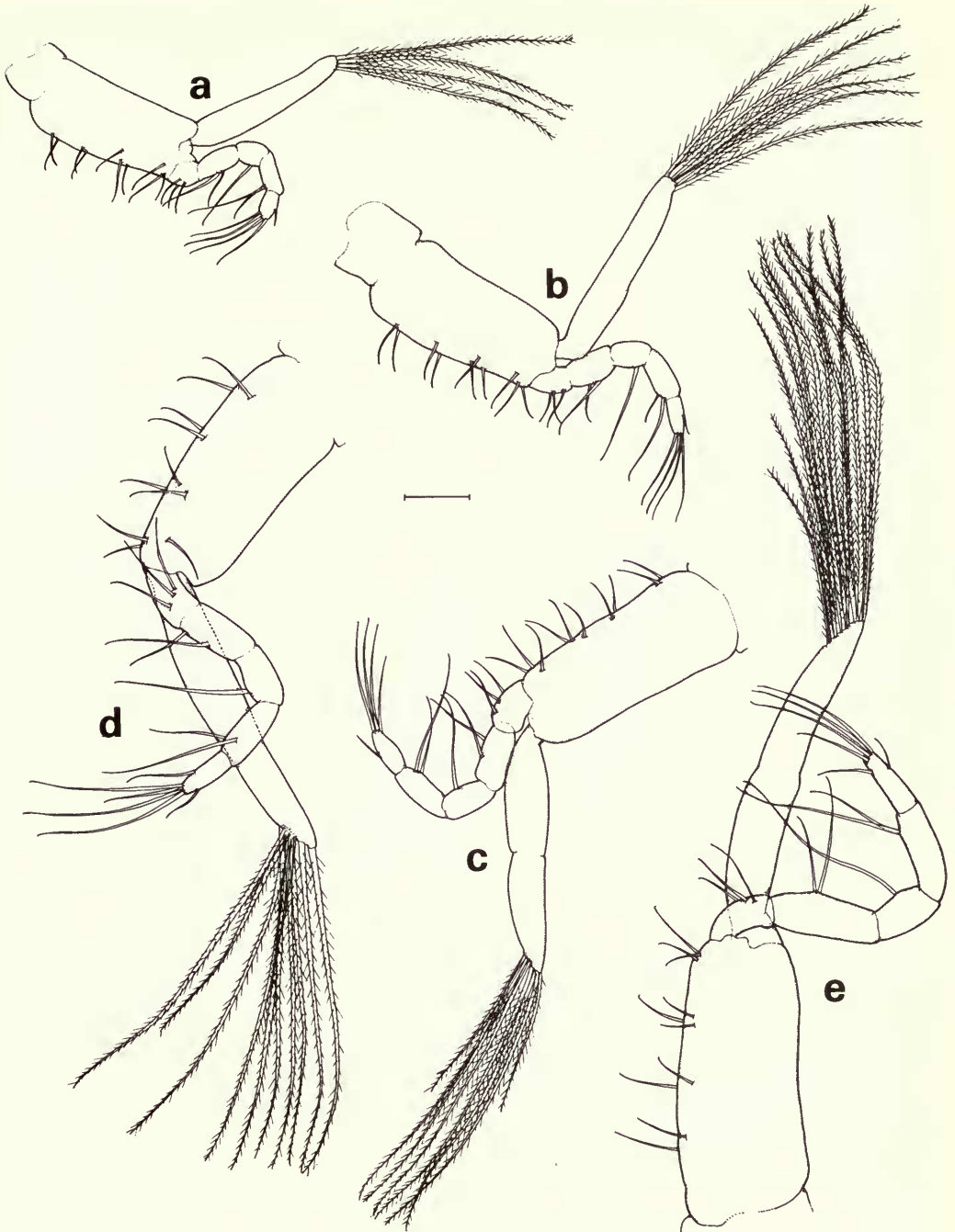
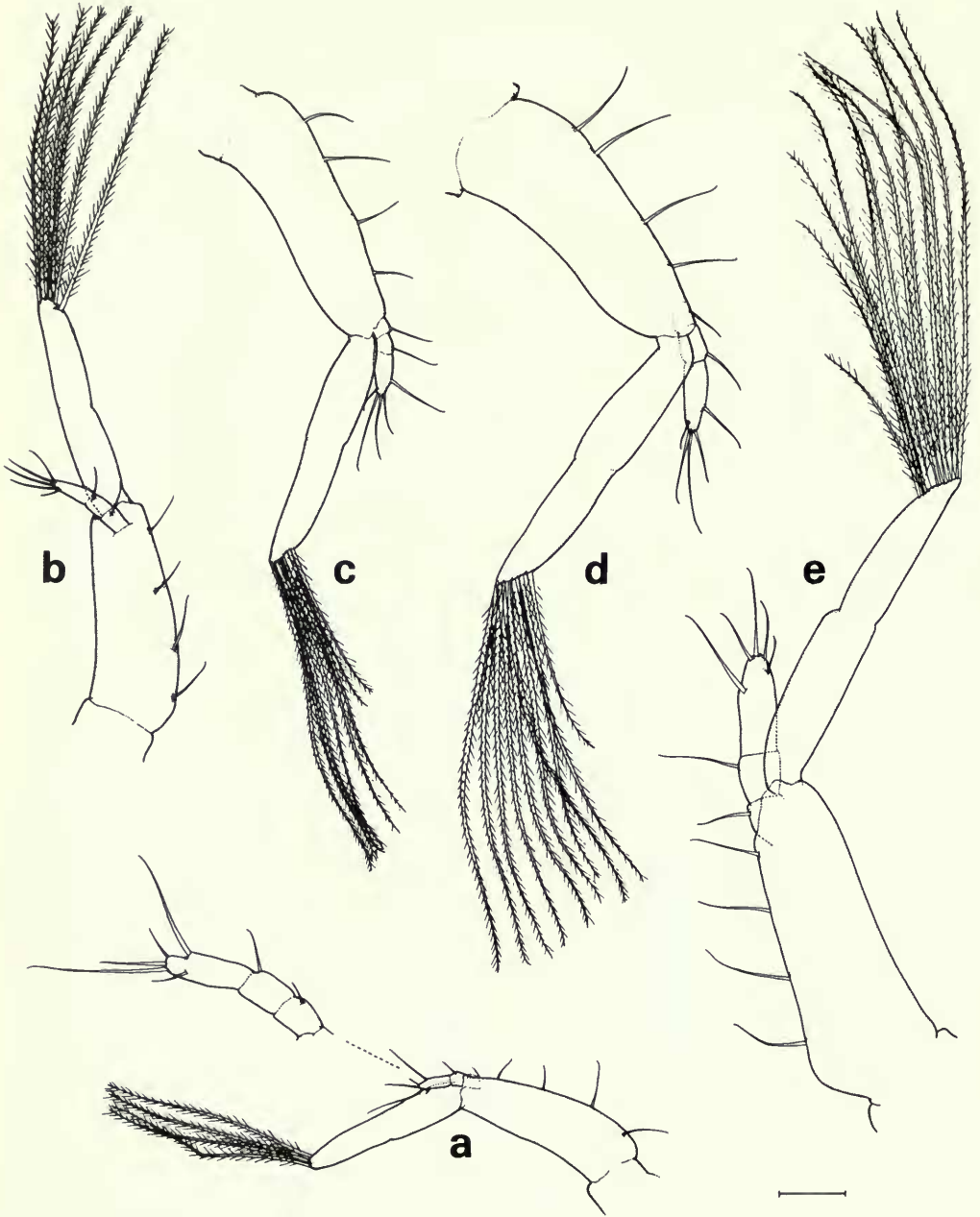
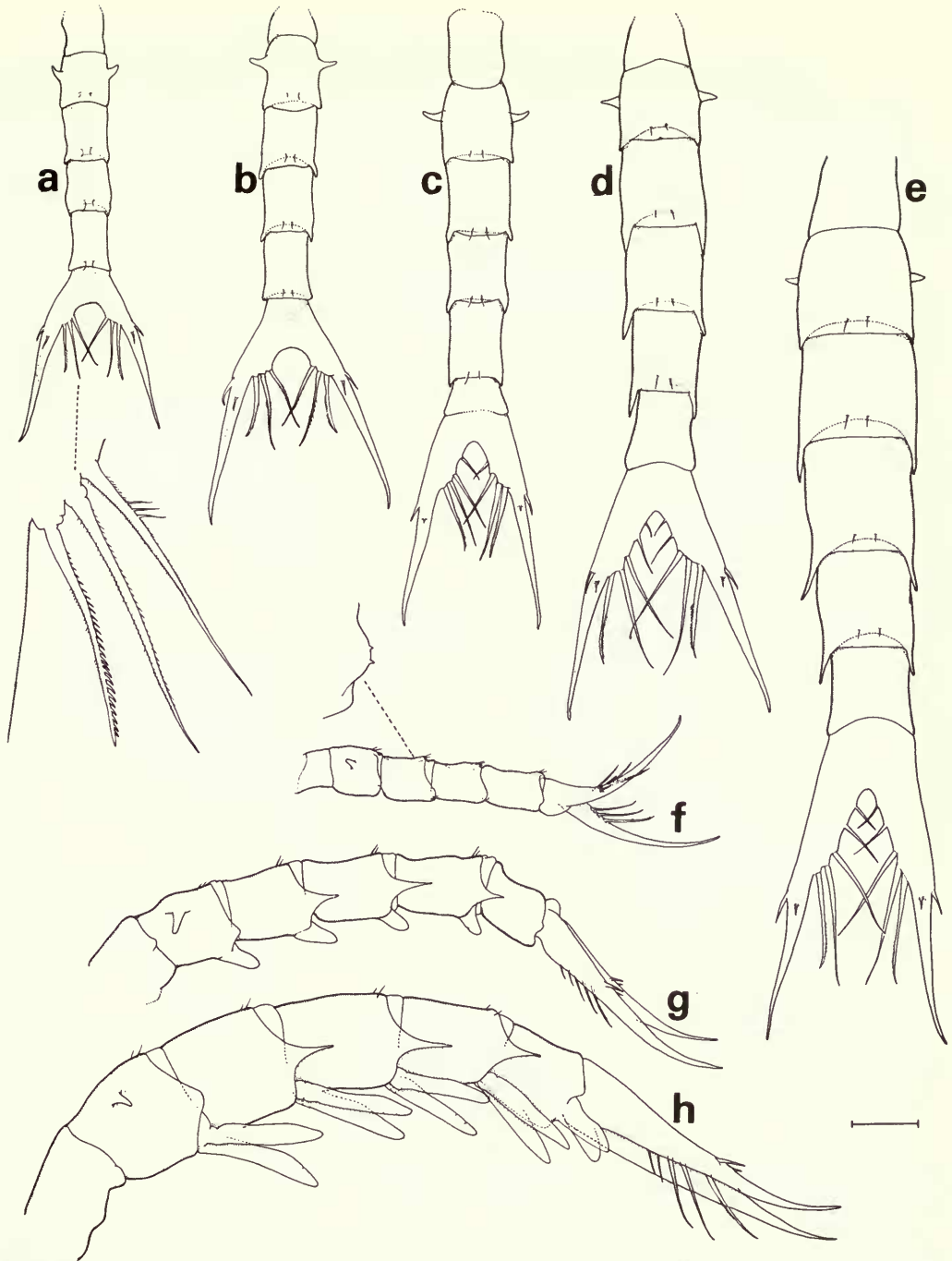


Fig. 6 *Cancer pagurus* L.: a-e first maxilliped 1st-5th zoeae; scale = 0.1 mm.



**Fig. 7** *Cancer pagurus* L.: a-e second maxilliped 1st-5th zoeae; scale = 0.1 mm (inset to a endopod of another specimen at higher magnification).





**Fig. 8** *Cancer pagurus* L., abdomen and telson: a-e dorsal aspect of 1st-5th zoeae; f-h lateral aspect of 1st, 4th & 5th zoeae; scale = 0.2 mm (inset to f postero-lateral margin of 3rd segment at higher magnification).

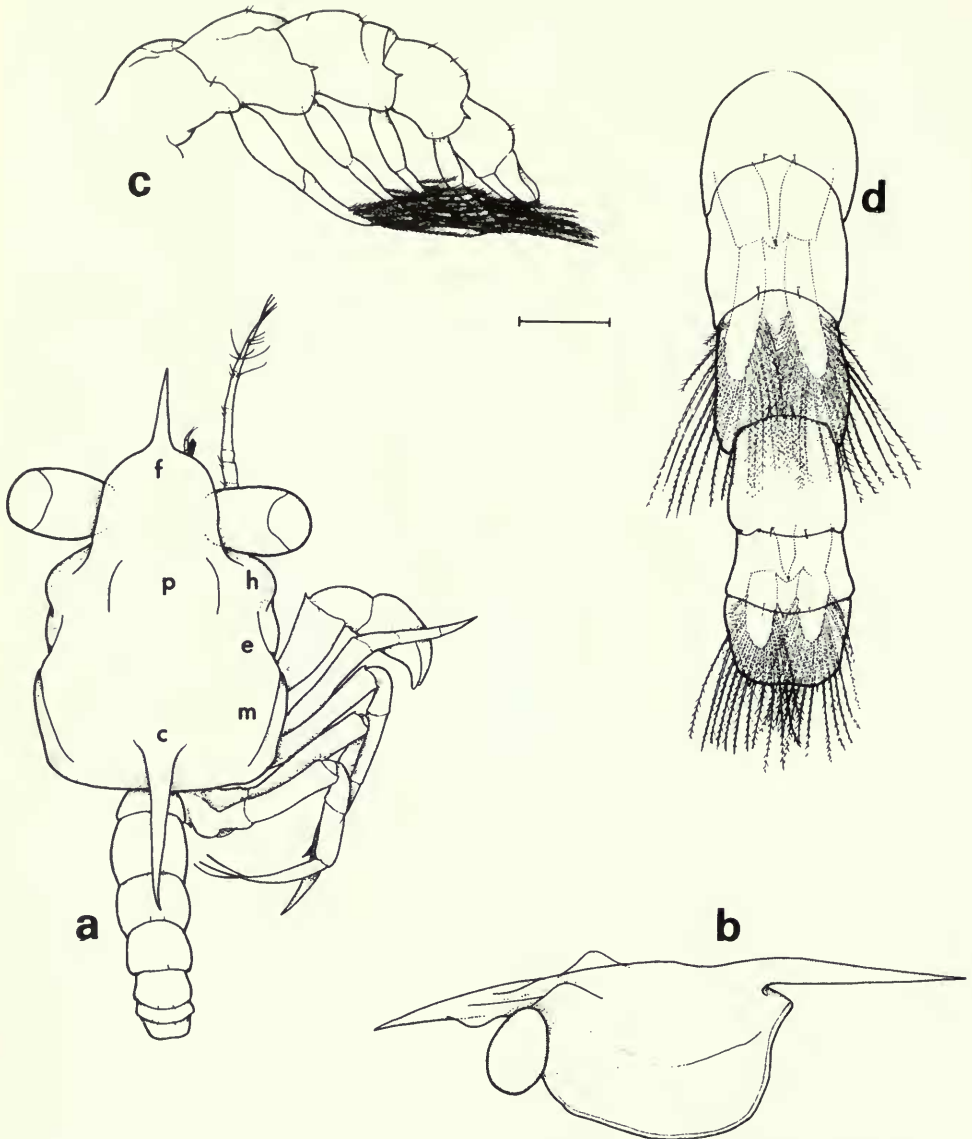
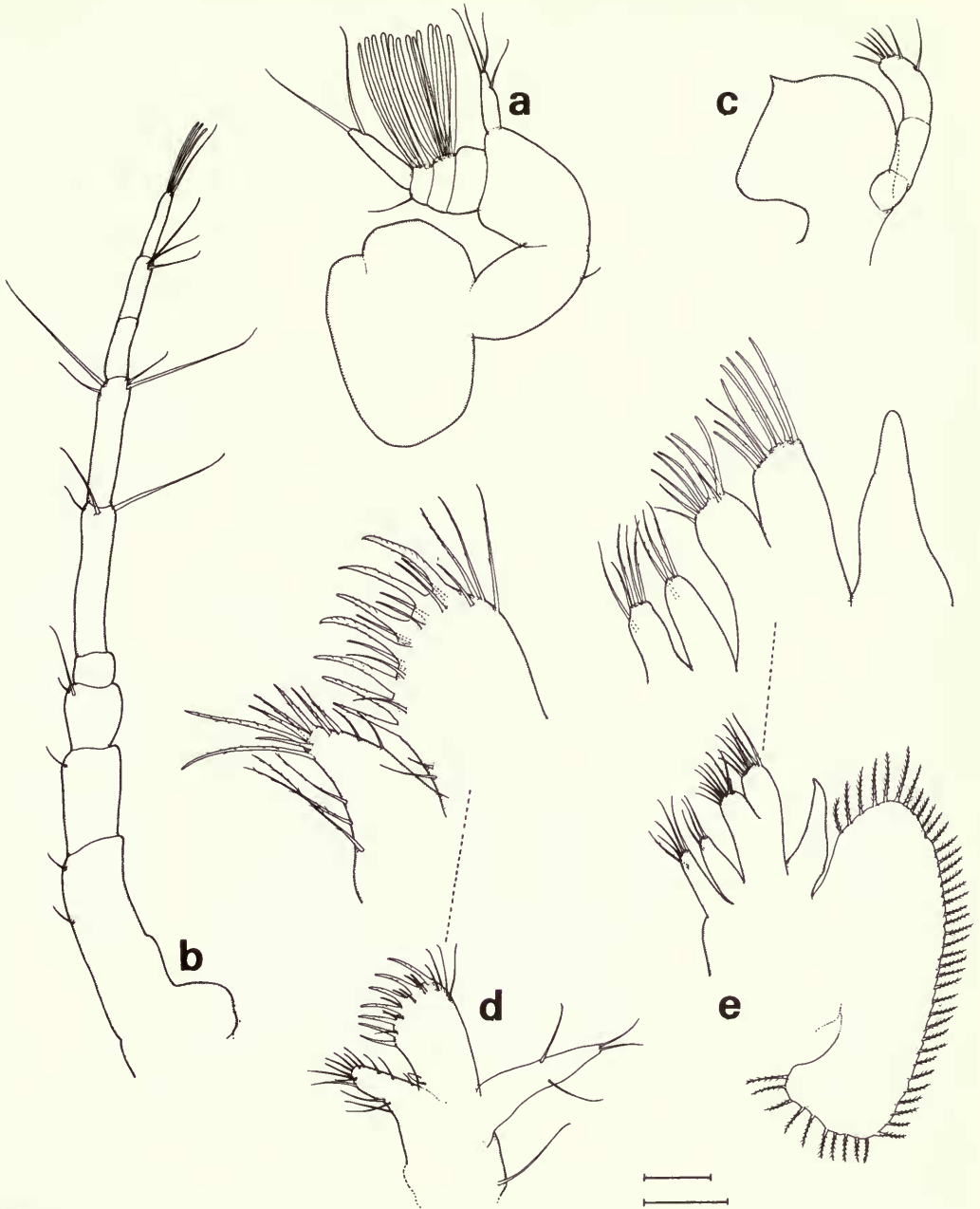


Fig. 9 *Cancer pagurus* L.: a dorsal aspect of megalopa; b lateral aspect of carapace; c-d abdominal segments 2-6 + telson from lateral & dorsal aspects (uropods omitted from d); c-d to scale 0.2 mm.

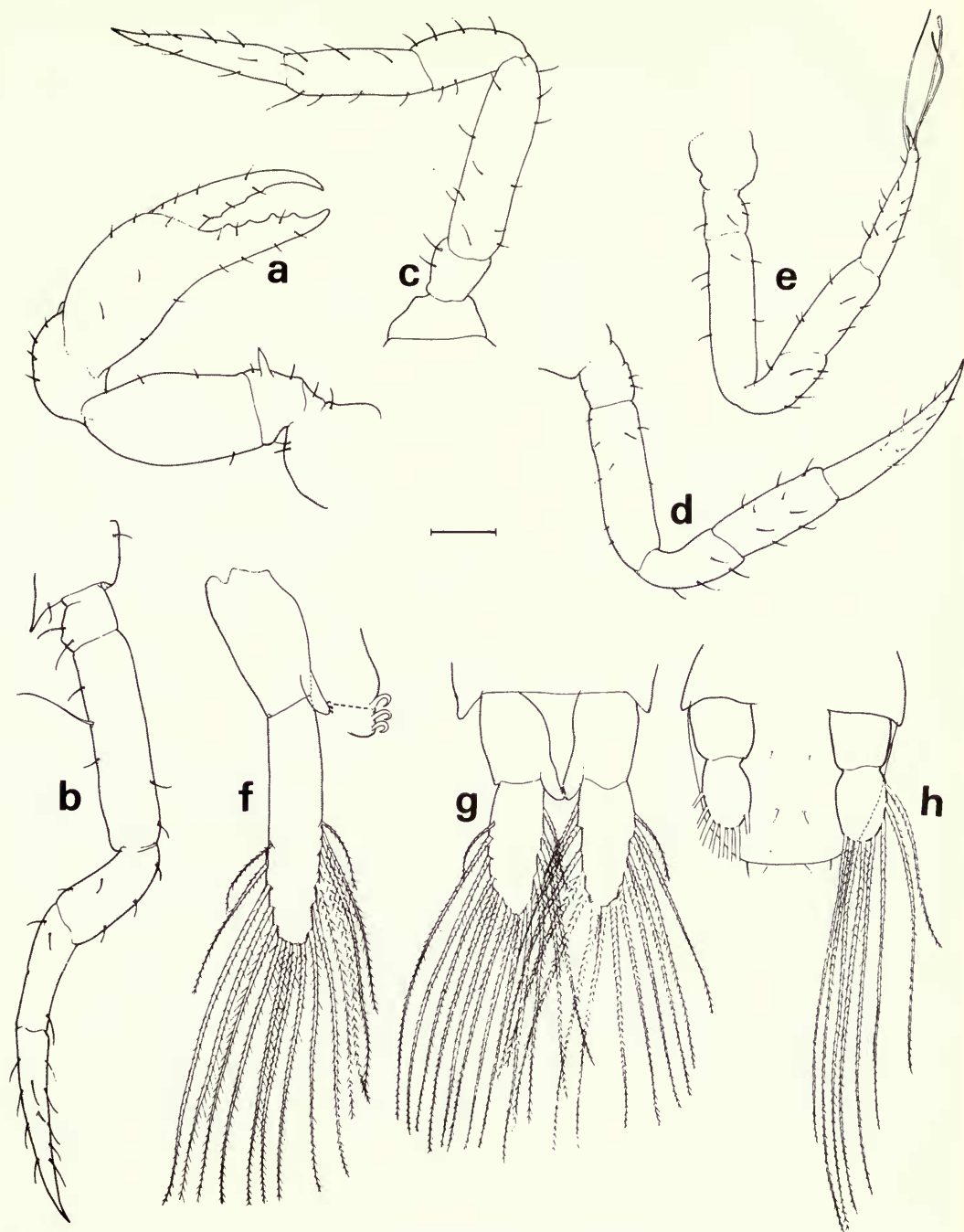


**Fig. 10** *Cancer pagurus* L.: a antennule; b antenna; c mandible; d maxillule; e maxilla of megalopa; whole appendages to upper scale = 0.1 mm., inset to lower scale = 0.05 mm.

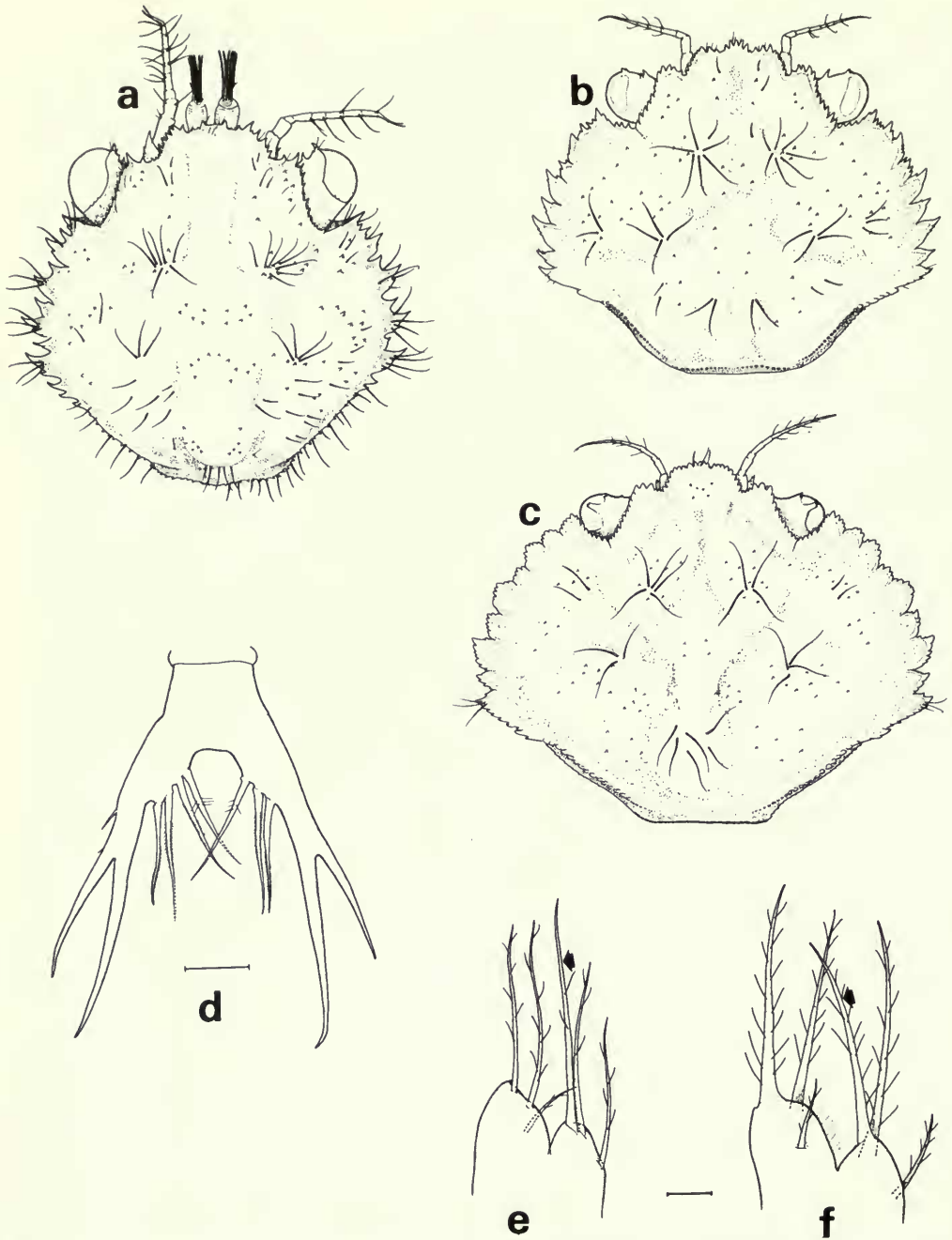


**Fig. 11** *Cancer pagurus* L.: a-c 1st-3rd maxillipeds of megalopa; whole appendages to left scale = 0.1 mm., insets to right scale = 0.05 mm.





**Fig. 12** *Cancer pagurus* L.: a-e 1st (= cheliped) to 5th pereopod; f 1st pleopod; g 4th pair of pleopods; h 5th pair of pleopods and telson from ventral aspects all of megalopa; scales a-e = 0.2 mm., f-h = 0.1 mm.



**Fig. 13** *Cancer pagurus* L.: a-c carapaces of 1st-3rd crab stages measuring 2.5 mm., 3.0 mm & 4.0 mm C.L. respectively; d abnormal telson of first zoea from S. North Sea; scale = 0.1 mm. Coxal lobes of maxilla of, e *C. pagurus* L.; f *Liocarcinus puber* (Linnaeus); scale = 0.01 mm.